BOOK REVIEW

Edward O. Wilson: *The Insect Societies.* Cambridge, Mass., Belknap Press of Harvard University Press, 1971. 548 pages. Illustrated with photographs and line drawings. Glossary, bibliography, and index. $20.00.

A book on insect societies written 50, or even 25, years ago would probably have carried the subtitle, Wonders of the Insect World, and would inevitably have lived up to its promise as a descriptive tract. But in the interim almost every scientist's wonder has turned inward, to find how sinews, nerves, and guts make organisms work. It has become a truism that song sparrows do not really sing; rather a surge of circulating hormones forces them to curse the competition in terms that only we outsiders find harmonic. I was afraid of finding Edward O. Wilson's *The Insect Societies* similarly introspective and sterile in its orientation, especially when a riffling of its pages exposed substantial numbers of graphs as well as a sprinkling of hopelessly technical mathematical formulae. But it did not turn out that way. To make his modern interpretations of mechanisms that regulate insect societies, Professor Wilson would have had to refer to a great body of descriptive lore in any case. However, he obviously takes as much joy in the free flight of a bee as he finds in a queen bee's ability to secrete *trans*-9-keto-2-decenoic acid to control affairs of the hive. Thus this extraordinary entomologist first dazzled me with a satisfyingly elaborate account of wonders of nature that *I* admire, and then succeeded in persuading me that *his* inquiries into the background of behavior involved topics that are equally wonderful.

Since I have just mentioned it as an example, I might as well report what Wilson reveals about *trans*-9-keto-2-decenoic acid. It has been known to students of bees for many years that workers in the hive constantly groom the queen by licking her. Even better known was the fact that bee colonies multiply by the process of swarming, at which time the old queen departs with part of the worker population to found a new colony, while one of her daughters supplants her as queen in the old hive. But it was not suspected that grooming and swarming were directly related phenomena.

The fact is that the workers' zeal for grooming their queen is not wholly altruistic. The queen secretes certain substances that the workers seem to crave. These so-called pheromones are then spread through the colony by the process of trophallaxis—regurgitation from one worker to the next—until the behavior of every member is controlled by chemical influences emanating from the queen. *Trans*-9-keto-2-decenoic acid is produced by the queen's mandibular glands. Its function is to prevent the workers from constructing queen cells. As long as each worker receives 0.1 μg. of the pheromone daily, only worker cells will be built. In late spring the old queen's production of the pheromone falls off, queen cells appear, and swarming duly ensues.

Does that seem unpleasantly intricate and dull? In a way it repeats the song-sparrow story by taking the glamor out of a cherished mystery. However, I can think of one person who would have been delighted by revelations of this kind. The celebrated entomologist Maurice Maeterlinck was horrified to note that termites practice trophallaxis in their colonies but that exchange of materials from termite to termite takes place from the anus. That fastidious observer could see nothing but depravity in such behavior, whereas it is now known to have several indispensable functions.

Then there is allometry. Not being a mathematician, I am always frightened when biology has to be dished up in formulae. But the subject of allometry was so engaging that I forced myself to understand what Wilson was trying to get across with the expression $y = bx^a$ which, he insisted, explained how the soldier caste in ants could have come into possession of such great jaws. I still think English is a better way to say these things, but in any case Wilson's formula boils down to the fact that if a equals 1 the proportions of parts of the body remain the same as sizes of castes vary. But if a exceeds 1, the particular part being measured will enlarge out of proportion to a given increase in body size. Of course the ants do not know anything about that, but somehow their genes do. In any event, evolution has been able to work on ants' genetic constitutions to produce gigantic jaws in soldiers that, without allometry, would have to be many sizes greater over-all to possess such formidable mouthparts.

I hope that I am conveying the message that this book is a joy to read for anyone who is *not* an expert. Maybe that is not what Professor Wilson intended, but he is now stuck with what I insist must be a

popular as well as technical review. His organization of the material makes it simple for the reader to find what he wants, sufficient unto his preferred depth within any subject, and then to skip to the next attraction. Illustrations and chapter headings serve as further beacons on this sea of abyssal deeps and refreshing reefs.

But I must not let my enthusiasm scatter my remarks in total disorder. I should first have said that Wilson's presentation is a model of precise organization. At the outset he carefully outlines the degrees to which insects associate, from solitary species that make contact only to mate and thereafter give no care to the young, through various intermediate states—subsocial, communal, quasisocial, and semisocial—to the most thoroughly integrated eusocial species. The latter aggregations comprise overlapping generations, with caste differentiation, all members collaborating in one way or another in colony affairs.

Eusociality is found among wasps, ants, bees, and termites, to each of which Wilson devotes a revealing review chapter. With this background established, he is then ready to plunge into problems of the development of castes and the evolution of various types of social behavior that castes immediately make possible by allowing specific duties to be relegated to the differently constituted individuals of a colony. Simultaneously a system of controls becomes necessary to ensure that the different individuals stick to what they are designed to do. Wilson consequently presents a general chapter on the elements of behavior, and then goes on to a lengthy discussion of communication. This is the point where modern discoveries overturn so many old beliefs when it is found that numerous items of communication between colony members are not mediated directly through the senses but result from the dispersal of chemical pheromones during food exchange and grooming.

The remaining chapters deal with several other aspects of sociality, including the myriad of opportunistic hangers-on that have succeeded in infiltrating colonies of all kinds and establishing themselves as symbionts of one sort or another within their protective limits. Some of the most bizarre creations in all nature are found in these situations, since the direction of each inquiline's evolution has now been turned from self-sustaining independence to self-ingratiating helplessness. Accordingly we find an illustration on page 407 depicting a beetle whose abdomen has been modified to resemble the complete body of its termite host. Moreover, this marvellously sculptured abdomen bears four

pairs of appendages, corresponding to the paired antennae and legs of the host, which are in reality "exudatoria," or glandular processes believed to produce substances that are attractive to the termites.

But social parasitism has taken place within the ranks of social insects themselves. One can easily conceive of the wandering beetle that blunders into a termitarium and decides to stay. But why should ants—or termites—sponge on each other? Everyone has heard of slave-making ants, but perhaps he has taken this trait more as a warlike act than as a true form of parasitism. Slave-making may indeed have arisen only as a means of temporarily increasing the labor force. Nevertheless the invasion of the nest of one species of ant by another has led in some cases to forms of dependence as extreme as those of the peculiar termitelike beetle just mentioned. On page 350 Wilson presents a drawing of a tiny ant whose queens are ectoparasites on the queens of their host species. These queens spend their entire lives clinging to the large queen, being fed by host workers when they feed their true queen. The parasites are highly attractive to the workers—again by virtue of their secretions. Each parasitic queen lays an egg every 30 seconds and, by some means, the host queen's eggs are rendered nonviable. Thus the host workers spend their time tending eggs, larvae, and pupae that will produce only additional parasitic queens and males, the parasitic worker caste having become suppressed as superfluous.

All these facets having been considered, Wilson is finally in a position to probe the population dynamics of colonial insect species. While some generalizations become possible, the truth remains that insect societies show a tremendous range of colony size, from a few dozen individuals among certain wasps and bees, to many millions in the case of some ants and termites. Death rates of individuals, and colony longevity as a whole, result from combinations of forces that are difficult to measure. It would appear, however, that there must be numerous advantages inherent in the colonial system, for the formation of societies has taken place independently many times. Termites, in fact, have many parallels among colonial ants—the development of a soldier caste, for example—although termites and ants are only remotely related in the insect world. Ants may be considered as wingless bees, whereas termites are only sophisticated cockroaches.

Wilson informs us that what entomologists have done to date is largely

descriptive; only today are scientists ready to make a beginning in the analysis and understanding of insect societies. The computer and the chemist will revitalize old concepts and generate new ones. The extraordinary privilege accorded us is to be present while this technical metamorphosis is taking place.

One is left with no doubt that E. O. Wilson loves his subjects. Evidence of his feelings appears again and again in his personification of these insects. The queen *who* does this, the slave *who* does that, and the larva *who* does something else all testify to the sentiments of the author who adores them, every one.

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